# The Pollen Morphology of Some Co-occurring Species of the Family Myrtaceae from the Sydney Region

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Myrtaceous pollen is superficially very similar so that the identification of dispersed grains is notoriously difficult. Given the importance of the family in the Australian vegetation, the identification of dispersed grains is extremely important for palynological studies on the history of the vegetation. This study examines means of a more precise and reliable identification of myrtaceous pollen.

A reference set of 20 species were analysed, from within an area used for palynological analysis and a historical vegetation study. A number of gross morphological and fine detail characters were scored. There are sufficient diagnostic character states to separate all but two of the species in which there is overlap. The success of this approach depends upon the inclusion of fine-detail characters.

The methods employed here use tables and keys as aids to identification but punch cards or a computer program would be equally suitable. Indeed, with a larger reference set, a computer program would be essential.

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## INTRODUCTION

Early studies on Myrtaceae pollen (e.g. Erdtman, 1952 and Pike, 1956) concluded that the family has more or less uniform pollen. Pike (1956) surveyed some 300 species from 71 genera and used the slight differences she observed to construct a tentative key to the genera. The key separates out some single genera but most of the end groups contain a number of genera, and one group contains 15 genera. Moreover, some genera, e.g. *Angophora* and *Eucalyptus* occur in 3 of these multi-generic groups. Clearly, this approach is unsatisfactory for the practical purposes of identifying dispersed pollen with a parent taxon. These earlier studies, however, concentrated on gross morphology.

In a more detailed study, McIntyre (1963) found that of 5 genera of Myrtaceae present in New Zealand, 3 could be distinguished individually. However, identification of species is difficult and usually not possible except for genera with only one species. This contrasts with Australia because the problem of identifying myrtaceous pollen is much simpler in New Zealand, which has only 18 native species.

In a study undertaken mainly for taxonomic purposes, Gadek and Martin (1981) examined 28 species of the subtribe Metrosiderinae. They found that the gross morphological characters, e.g. syncolpy or parasyncolpy, presence or absence of a polar island, may not be taxonomically reliable at the species level. The characters most useful in assessing taxonomy were those of fine detail, e.g. the structure of the angle of the amb, exine structure and sculpture, form and type of colpi and apocolpia. Using these characters, some species were distinctive enough to be identified from all others in that study.

The identification of dispersed myrtaceous pollen is of paramount importance for palynological studies into the history of the Australian vegetation. Altogether there are some 47 native genera and 1300 species of this family in Australia (Beadle, 1981). *Eucalyptus* is dominant over much of the Australian continent outside of the arid

Eremaean Zone and the small, discontinuous area of rainforest. Although not dominant in the Eremaean Zone, *Eucalyptus* is far from uncommon there. In rainforest, other genera in the family may be important. Vegetation units are defined in terms of their dominants. If past vegetation, as deduced from pollen spectra, is to be defined with any sort of precision, then the problem of identifying dispersed myrtaceous grains must be tackled.

There are some Quaternary palynological studies that differentiate myrtaceous pollen into groups. The most successful of these is that of Churchill (1957, 1961 and 1968) who distinguished 7 species of *Eucalyptus* and a group of 2 species which are closely related and hybridize freely. Churchill (1957) used ten character states of both gross morphology and fine detail. These included equatorial diameter, polar axis, sexine sculpture, presence of polar islands, depth of colpi, concavity of sides of amb, comparative thickness of the sexine and nexine and several pore characters. This study, using many more characters than any other, has been very successful. However, this approach has been ignored by subsequent workers in the field.

Dodson (1974) used 4 characters to place 27 species of 8 genera into 13 groups. Two of the characters are those of fine detail, viz. pore type and nature of the colpus. The other 2 are those of gross morphology, viz. presence or absence of a polar island and equatorial diameter. The 12 *Eucalyptus* species in that study were placed in 4 groups and one of these is a single species. There are 3 other single species groups. In subsequent works, Dodson (1977, 1979, 1982) continued this approach. Binder (1978), using the same 4 characters of Dodson, divided 30 species into 9 groups, 3 of which are *Eucalyptus* groups. Only 2 of these groups are single species, and they are not eucalypts. Rose and Martin (in prep.) use much of the same characters to define 4 groups within the Myrtaceae, 2 of which are *Eucalyptus* and *Angophora.*

Ladd (1979) divides the *Eucalyptus* species in his area of study into 5 groups without any indication as to how this division has been achieved. Not a single groups is exclusive, i.e. at least one species in each group is found in another group. Most other Quaternary studies attempt little subdivision of the myrtaceous pollen, e.g. Colhoun *et al.* (1982) with 2 groups, one of *Eucalyptus/Melaleuca* species, the other of *Leptospermum* species.

In summary, the previous studies show that subdivision and identification of dispersed myrtaceous pollen may be successful if the fine detail characters are used, together with those of gross morphology. Greater success has been achieved using a larger number of characters.

This paper explores the feasibility of specific identification of myrtaceous pollen in the reference set. Variation within a species has been assessed as well as the definition of diagnostic character states of a species or group of species.

The reference set of 20 species comprising those found in the Jibbon Swamp area of the Royal National Park, with a few specimens not actually growing in the region but included as possible occupants of the area in the past. A palynological study of Jibbon Swamp and the history of the vegetation (Chalson, 1983) relies on the identification of the myrtaceous pollen.

## Method

Dry anthers have been collected from herbarium specimens in either the John T. Waterhouse Herbarium, University of N.S.W. (UNSW) or the National Herbarium, Royal Botanic Gardens, Sydney (NSW) (Table 1). The anthers have been treated according to Erdtman's acetolysis method as modified by Chanda (1966). The treated pollen has been mounted in safranin/glycerine jelly. This mounting medium is preferred because the slight expansion it causes, when compared with silicone oil, allows the layers of the exine to be seen more clearly. Pollen grains which have been mounted in glycerine jelly for a long period of time may swell (Anderson, 1960) for this reason most of the pollen slides used were mounted within the last two years. Some slides from the modern reference pollen collection at the Botany School, University of N.S.W. were included, but only after selection to preclude swollen grains. Photomicrographs have been taken using a Zeiss microscope, x100 lens (n.a.1.3) under oil immersion and through a green filter. Observation has been carried out with the same set-up without the green filter.

Measurements are based on at least 20 grains; the mean measurement is enclosed in parenthesis between the range observed. The measurements are in micrometers (μm).

Herbarium specimens used for obtaining pollen for analysis are listed in Table 1. All pollen slides have been placed in the collection at the Botany School, University of N.S.W. Palynological terms are defined in Kremp (1965) unless otherwise stated.

## Generalised Pollen Morphology

The grains are free, radiosymmetric, isopolar or almost isopolar, oblate, triangular, angulaperturate and tricolporate. Two layers in the exine are usually distinguishable, the endexine and ektexine, both more or less of equal thickness (Fig. 1).

The equatorial apertures are complex and are formed by a splitting of the endexine and ektexine to form a vestibule. In equatorial view the vestibule appears as a meridional colpus in the ektexine when viewed from the surface, and is elliptical to slit-like in shape. The endexine viewed through the equatorial colpus appears granular if the inner surfaces of the vestibule are roughened. The endexine appears to have an indistinct equatorial colpus. In polar view the roof and the floor of the vestibule are extensions of the ektexine and endexine layers, respectively, of the exine. Whilst the floor is usually the same thickness as the rest of the endexine, the roof may be thicker, thinner or the same width as the ektexine elsewhere on the grain (Fig. 10).

Most grains settle in the polar aspect due to the extreme oblate shape, thus all observations have been made from the polar view and the equatorial endocolpus is not visible. If the ektexine is markedly thickened or patterned over the vestibule, the equatorial colpus may not be visible, and the whole of the pore may be partially obscured, or indistinct. Very small vestibules with little separation of the ektexine and endexine may also be indistinct in polar view.

The morphology of the polar region varies greatly both between species and, in some groups, within species. Grains may be syncolpate, parasyncolpate, brevicolpate or syndemicolpate (Fig. 6). The apocolpium may be covered with ektexine (a polar island) or an expanded membrane (Gadek and Martin, 1981) similar to that of the colpi (Fig. 5).

Exine patterning is generally fine, most species being scabrate or smooth. Patterning often changes along the colpi edges and over the pore areas.

Abnormal grains are found in all species. There are two common forms of abnormality. Some grains have 2, 4 or 5 pores instead of the normal 3 (Fig. 12S) which does not appear to affect the other character states of the grain used for identification, and thus these grains can be ascribed to a species if they have the correct orientation. The other common abnormality occurs when grains have very thick exine. These grains are usually smaller than the normal range and have strongly concave or convex walls. These grains are not identifiable.

## The Characters

The pollen grains range from concave triangular through straight triangular to convex triangular (Fig. 3). The angle of the amb may be sharply rounded or rounded, and there may be a notch at the base of the vestibule (Fig. 4).

The polar region displays a variety of character states. The colpi may not meet at the pole, or only one colpus may bifurate (Fig. 9). The apocolpium may be covered with ektexine (a polar island) similar to elsewhere on the grain, more highly patterned than elsewhere or thinner and less patterned than elsewhere on the grain. The apocolpium may, alternatively, be an expanded membrane similar to that of the colpi and either smooth or with scattered granules on the surface (Fig. 5C). Polar islands may either fit closely into the apocolpium (i.e. have the same shape and almost the same size) or they may be smaller than the apocolpium and have an irregular shape (Fig. 5A, B).

The pore area is similarly complex and variable. In all cases some degree of splitting of the endexine and ektexine is visible. However, visibility may be impaired by thickened ektexine over the roof of the vestibule, rough inner surfaces of the vestibule, continuation of the exine patterning over the vestibule roof, small size of the vestibule and/or strong colouring of the exine. The floor of the vestibule is a continuation of the endexine elsewhere on the grain. It may be concave, flat or convex and is generally the same thickness as the endexine elsewhere on the grain (Fig. 10). The roof of the vestibule is smooth or patterned on the outside. Although the roof is a continuation of the ektexine elsewhere on the grain, the surface pattern usually changes over the immediate pore area. The thickness of the roof may either taper gently towards the exopore, round off abruptly or be truncate at the exopore edge. The inner surfaces of the vestibule are either rough or smooth (Fig. 10). The measurement of pore height is external, it includes both the floor thickness and roof thickness. The measurement of pore width is internal as the inclusion of wall thickness would make the measurements too variable to be of use (Fig. 2). Grains must be viewed in true polar view otherwise the character states associated with the pore area will not be seen clearly.

The elements of the exine patterning are generally less than 1 μm., i.e. scabrate (Erdtman, 1952). However, different shaped elements are clearly visible, even at this small size, and they are described as smooth, undulate (Fig. 11B), scabrate, verrucate/scabrate, granulate/scabrate, granulate, verrucate, vermiculate or rugulate (Fig. 11). The term scabrate is reserved for a very rough irregular form of scabrate patterning. There is variation in the distribution of exine patterning. Patterning may be found evenly distributed over the whole grain, more commonly it is absent or reduced around the pore area. In addition, patterning may be restricted to the equatorial mesocolpal areas or it may be most pronounced along the edges of the colpi.

Colpi may have gaps where the colpus is not visible and normal ektexine is found occupying the gap instead (Figs 8, 9). Some colpi have thickened borders, others have broken, rough, irregular or smooth edges (Fig. 7). Broken edges have pieces of normal ektexine closely associated with the edges of the colpi but not attached to the mesocolpal region. Rough edges are continuously uneven but have no detached sections of ektexine. Irregular edges have infrequent, irregular sharp bends and smooth edges follow even curves or only bend at bifurcation points between colpi and poles.

The thickness of the wall is also measured (Fig. 2).

## Description of the Species

*Angophora hispida*

Grains have slightly concave sides and rounded ambs. The amb has a notch at the base of the vestibule. Colpi are usually arcuate with a distinct polar membrane approximately 5-10μm. The apocolpium rarely contains a polar island which is found on one side of the grain only. The edges of the colpi are broken. The colpi do not always extend from the pole to the pore but often have gaps and other irregularities around the immediate polar area (Table 7, Figs 8, 9). The exine is very thick. The surface is smooth with a slightly undulatory appearance in the optical section in the mesocolpal areas (Fig. 12A).

The pore areas protrude from the rest of the grain. The vestibule is small, and not always distinctly visible, and the inside surfaces are obviously roughened. The floor is flat, the roof is thickened and tapers abruptly at the exopore opening with rounded edges (Fig. 10D). The outside surface is smooth. Dimensions are in Table 3.

*A. hispida* is distinguished from most species by its large apex/base measurement. It does not have the grooved pattern of *A. costata* or *E. eximia.* More difficulty is experienced with *E. gummifera.* While some of the grains may be identified with their respective species there is overlap of all the character states (Table 3). Thus it is not possible to assign all the grains to a species.

*Angophora costata*

Grains have straight to slightly convex sides. The amb is rounded and notched at the base of the vestibule. Colpi are arcuate, syncolpate or with a very small polar membrane of about 1-2μm wide. The colpi may have gaps or very small polar islands (Table 7) and irregular edges (Fig. 7B). The exine has a smooth unthickened band, about 6μm wide, following the colpi. The mesocolpal areas are clearly patterned with vermiculate grooves (Fig. 11A). Grains seen in oblique polar view are rarely deformed, giving the impression of a strong rigid wall (Fig. 12B).

The amb has a small distinct vestibule with rough inner surfaces. The floor of the vestibule is concave in polar view. The ektexine over the vestibule is conspicuously thickened, but thins abruptly towards the rounded edges of the exopore and is smooth on the outer surface (Fig. 10D). Dimensions are in Table 3.

This species is clearly distinguished from *Angophora hispida* and *Eucalyptus gummifera* by the distinctive, grooved pattern in mesocolpal regions (Table 3). *A costata* is distinguished from *E. eximia* by its apex/base measurement.

*Eucalyptus botryoides*

Grains have straight to concave sides. The amb is rounded and notched at the base of the vestibule. Colpi are straight and angular (Fig. 6C) with rough margins, enclosing a polar island 4-9μm wide. The polar island closely fits the apocolpium. Exine patterning is finely scabrate and distributed evenly over the entire grain except the pore areas which are smooth.

The amb generally has a narrow vestibule, a rough inner surface is visible on some of the specimens with wider vestibules. The floor of the vestibule is straight to slightly convex. The ektexine over the vestibule is very conspicuously thickened and is smooth on the outside. The ektexine thins abruptly at the exopore and has rounded edges (Fig. 10B). Dimensions are in Table 3.

This species is distinguished from the *Angophora*/bloodwood group by its fine scabrate pattern on the exine. It differs from the other species of the *Eucalyptus* group by a large polar island with the same patterning as that of the ektexine elsewhere on the grain (Table 4). This species is distinguished from the *Melaleuca* group by its large polar island, scabrate patterning, angular colpi and rough colpi edges (Table 2).

*Eucalyptus camfieldii*

Grains have straight to slightly concave sides and rounded ambs. Colpi are straight and angular with rough edges (Fig. 7C); the bifurcations enclose a large, triangular polar membrane 8-9μm wide, which lacks ektexine. The ektexine has a faint scabrate pattern which is more pronounced on the equatorial mesocolpium. The less patterned ektexine forms a band approximately 5μm wide along the colpi edges. Most of the grains are seen in an oblique angle indicating a less extreme oblate shape than is the norm for the Myrtaceae species studied here. The polar region is frequently depressed probably because the lack of ektexine makes it less rigid. With the depression of the polar membrane, the surrounding areas tend to cave in around it, making clear viewing of the polar region difficult.

The amb has a distinct vestibule, the inner surfaces of which appear to be roughened. The floor of the vestibule is straight or slightly concave in pores in true polar view, but may appear convex if viewed at an oblique angle. The ektexine over the vestibule is conspicuously thickened and smooth on the outer surface.

The depressed polar region is characteristic. Dimensions are in Table 3.

This species is separable from the *Angophora*/bloodwood group by its scabrate pattern. It differs from the rest of the *Eucalyptus* group by having both a smooth polar membrane and a thickened vestibule roof (Table 4).

*Eucalyptus eximia*

Grains have concave to straight sides, the amb is rounded and notched at the base of the vestibule. Colpi are accurate with very rare gaps (approximately 7.5% of the sample) which are less than 1μm long (Table 7). The sides of the colpi are rough and irregular and not thickened (Fig. 12D). Frequently the apocolpium has a small polar island which may be irregular in shape (Fig. 5B) or may closely fit the apocolpium. The apocolpium is approximately 4-8μm across with ektexine granules when a polar island is absent. The ektexine is rugulate or rugulate/scabrate.

Ambs have medium sized, indistinct vestibules with rough inner surfaces. The floor of the vestibule is flat, the roof is thickened (Fig. 12C) when compared to the rest of the ektexine and is patterned on the outside. The roof tapers abruptly towards the exopore and has rounded ends (Fig. 10D). Dimensions are in Table 3.

The vermiculate grooves separate this species from most other Myrtaceae pollen. *Angophora costata* is much larger and *Eucalyptus obstans* has angular colpi and no colpi gaps.

*Eucalyptus gummifera*

Grains have straight to slightly concave sides, the amb is rounded and notched at the base of the vestibule. Colpi are usually arcuate enclosing an apocolpium up to 10μm in diameter, however, the polar region is very variable (Fig. 9). The colpi have broken edges (Fig. 7D), they may be continuous, or one or more may have a gap from 1 to 5μm long (Fig. 12F), where the colpus appears to end and normal ektexine occupies the area. There is also variation in the way the colpi meet at the pole. There may be a polar island or a partially separated island or an island not separated at all (Fig. 9). This variation is discussed further below under intraspecific variation. The exine is undulate in the equatorial mesocolpal region (Fig. 11B).

There is a small indistinct vestibule with roughened inner surfaces while the floor is straight to slightly convex (Fig. 12E). The ektexine over the vestibule is thickened and smooth on the outer surface. The roof tapers abruptly towards the exopore and has rounded edges. Dimensions are in Table 3.

This species is morphologically close to *Angophora hispida* and most character states overlap between species (Table 3). Thus while some of the grains may be identified with their respective species, it is not possible to assign all of the grains confidently.

*Eucalyptus haemastoma*

Grains have straight to slightly concave sides, the amb is rounded and notched at the base of the vestibule. Colpi are straight and angular with rough edges (Fig. 12H). The colpi bifurcate to form a large apocolpium approximately 5-8μm wide. A large polar island fills the apocolpium almost entirely. The polar region is best observed in fully expanded grains because the expansion allows the colpi and the edge of the polar island to be seen clearly. The ektexine of the polar island is not the same as the rest of the grain, it is thinner and has a rugulate pattern, or it may consist only of granules (Fig. 5C). Exine is smooth to faintly scabrate. The endexine is approximately half the thickness of the ektexine. The pattern is uniform over the grain excluding the pore area.

There is a large and indistinct vestibule with rough inner surfaces. The floor of the vestibule is flat, the roof thickens between the edge of the vestibule and the exopore opening where it thins abruptly (Fig. 12G), the edge is rounded. The outer surface is smooth. Dimensions are in Table 3.

This species is separable from the *Angophora*/bloodwood group by its smaller size. It differs from the rest of the *Eucalyptus* group by a combination of the notched amb at the base of the vestibule, angular colpi, an exine pattern which extends over all of the grain excluding the pore area and a small pore height (Table 3).

*Eucalyptus luehmanniana*

Grains have straight to slightly concave or convex sides. The amb is rounded. Colpi are arcuate, the edges are rough and enclose an apocolpium 5-8μm wide. The polar region is one of two types; either the apocolpium contains a polar island 3-6 μm wide (which has thinner ektexine with granules (Fig. 12J)); or the colpi merge into an area of strong rugulate patterning of normal ektexine (Fig. 11G). The polar island is found on one side only and no specimens with polar islands in both sides were observed. Exine is smooth or faintly scabrate (Fig. 12I). The patterning is most pronounced at the colpal edges.

There is a small indistinct vestibule with rough inner surfaces. The floor is straight and the roof is thickened when compared to the rest of the ektexine and tapers abruptly to rounded edges at the exopore. Dimensions are in Table 3.

This species is distinguished from the *Angophora*/bloodwood group by its smaller size. It differs from the rest of the *Eucalyptus* group by rounded angles, arcuate colpi and exine patterning which is most pronounced at the colpal edges (Table 4).

*Eucalyptus obstans*

Grains have straight to slightly concave sides, the amb is rounded and notched at the base of the vestibule. Colpi are straight and angular, enclosing a large polar island which fits the apocolpium closely and is 7-9μm in diameter (Fig. 5A). The edges of the colpi are broken towards the pole, gradually becoming rough towards the pores. The ektexine of the polar island is thinner than elsewhere and may be covered with scattered granules. Exine patterning is vermiculate, the grooves run radially outwards from the polar region (Fig. 12L). The patterning is more pronounced at the colpal edges.

The amb has an indistinct vestibule with roughened inner surfaces. The floor is straight or slightly convex, although if viewed obliquely, it may appear concave. The roof of the vestibule is conspicuously thickened compared to the rest of the ektexine (Fig. 12K), and the whole of the pore has a heavy protruding look. The roof thins abruptly to rounded edges at the exopore. The outside of the roof is smooth. Dimensions are in Table 3.

This species is distinguished from all the other species in the *Eucalyptus* group by the radial grooves of the vermiculate exine pattern (Table 4).

*Eucalyptus sieberi*

Grains have straight sides (Fig. 3C), the amb is rounded and notched at the base of the vestibule. Colpi are curved enclosing an apocolpium approximately 4μm diameter. The edges of the colpi are rough. Exine has a fine scabrate pattern (Fig. 12N). The ektexine around the colpi is smooth.

There is a conspicuous vestibule, the inside surface is smooth. The floor is straight or almost so. The ektexine is the same thickness over the vestibule as that around the entire grain, thinning gradually to the edges of the exopore (Figs 10A, 12M), and is smooth over the vestibule. On some of the grains the areas surrounding the polar region cave in over the weak, polar membrane so that it is obscured. Dimensions are in Table 3.

The species is distinguished from the rest of the *Eucalyptus* and *Angophora* species by a thin roof and smooth inner surfaces of the vestibule (Table 4).

*Leptospermum arachnoides*

Grains have concave sides (Fig. 3B) and sharply rounded ambs. Colpi are straight and do not meet at the pole (Figs 6D, 12O). The colpi extend between half and two thirds the distance between the pore and the pole. The edges of the colpi are smooth and not thickened. The endexine is smooth and narrow. The ektexine is thicker (approx. 1.2μm) and has a strong verrucate pattern (Fig. 11C). The verrucae are 1.5 to 2μm in diameter over most of the grain but become smaller in both diameter and thickness (and thus verrucate/scabrate) towards the amb (Fig. 11D).

The vestibules are difficult to distinguish due to the intense patterning of the ektexine over the amb. The vestibule is small and the inside surfaces are very slightly roughened. The floor of the vestibule is flat and the roof thins slightly towards the exopore and has a smaller element size of the ektexine patterning. Dimensions are in Table 6.

This species is separated from the rest of the *Leptospermum* group by its verrucate patterning and by its colpi which do not meet at the pole (Table 6).

*Leptospermum trinervium*

Grains have straight to slightly concave sides and sharply rounded ambs. Colpi are straight, angular and syncolpate (Fig. 6A). The edges are not thickened and are rough. The apocolpium is less than 0.5μm wide. The ektexine has a granular pattern, granules < or = 1μm wide (Fig. 11E).

Ambs have small distinct vestibules with smooth inner surfaces. The floor of the vestibules is straight or almost straight and the ektexine over the vestibule is the same thickness as elsewhere on the grain. The outer surface of the pore has a granular pattern. The roof of the vestibule distinctly curves inwards at the exopore and does not thin. The pore is so small that its structure is distinct only on the best specimens. Dimensions are in Table 6.

This species is separated from the rest of the *Leptospermum* group by a combination of rough colpi edges and smooth inner surfaces of the vestibule (Table 6).

*Leptospermum polygalifolium*

Grains have concave sides and sharply rounded ambs (Fig. 4A). Colpi are straight, angular and syncolpate, the edges are not thickened and are smooth and there is usually no apocolpium. The ektexine has a fairly rough and irregular scabrate pattern over the entire grain.

Ambs have small vestibules with rough inner surfaces. The floor of the vestibule is slightly convex. The roof of the vestibule is the same thickness as the ektexine elsewhere on the grain and has the same scabrate patterning of the ektexine. The roof of the vestibule distinctly curves inwards at the exopore opening and does not thin. Dimensions are in Table 6.

This species is distinguished from *Leptospermum arachnoides* by its syncolpy and the scabrate patterning on the exine. This species is separated from the rest of the *Leptospermum* group by the combination of smooth colpi edges (Fig. 7A) and rough inner surfaces of the vestibule (Table 6).

*Leptospermum juniperinum*

Grains have concave sides (Fig. 3A) and sharply rounded ambs. The colpi are exceptionally difficult to see and are not visible on all specimens. Colpi are straight, angular and usually syncolpate. The edges are not thickened and are smooth. Colpi are variable, sometimes they have gaps or do not meet at the pole. The exine is smooth.

Vestibules are difficult to distinguish but good specimens reveal a convex floor slightly narrower than the endexine elsewhere on the grain. The roof of the vestibule is thin and may thin further towards the exopore or it may remain the same thickness. When visible, the inside surfaces of the small vestibule are smooth. Dimensions are in Table 6.

This species is distinguished from the other members of the *Leptospermum* group by its smooth exine pattern (Table 6).

*Leptospermum laevigatum*

Grains have straight to concave sides and the ambs are sharply rounded. Colpi are straight, angular and usually syncolpate with the edges rough and not thickened (Fig. 12P). An apocolpium may expand slightly to 2μm towards the pole. Gaps in the colpi may be present but they are rare. Ektexine has a granular/scabrate pattern with rounded and regular elements over the grain but not extending across the immediate area of the vestibule.

There is a narrow vestibule with a concave floor. The roof is the same thickness as the ektexine elsewhere and smooth on the outside. The roof does not thin towards the exopore and is truncate. The inner surfaces of the vestibule are rough (Fig. 10C). Dimensions are in Table 6.

This species is separated from the rest of the *Leptospermum* group by a combination of rough edges of the colpi and rough inner surfaces of the vestibule (Table 6).

*Melaleuca armillaris*

Grains have concave sides and rounded ambs (Fig. 4B). Colpi are arcuate (Fig. 6B) enclosing a small apocolpium, up to 2μm wide, the edges of the colpi are smooth. The colpi have distinct, narrow, thickened borders (<1μm wide). The exine is smooth.

The amb has a distinct vestibule with conspicuously roughened inner surfaces. The floor of the vestibule is straight or slightly convex. The ektexine over the vestibule is generally the same thickness as elsewhere on the grain but on some specimens it appears to become thinner towards the exopore.

There is considerable variation of the vestibule roof. On some grains the ektexine covering the vestibule tends to project outwards on one side of the exopore which suggests that the roof of the vestibule is somewhat fragile and subject to deformation. The floor of the vestibule, however, maintains its shape. Dimensions are in Table 5.

This specimen is most like *Melaleuca ericifolia* but may be distinguished by the more concave sides and larger, more conspicuous pore (Table 5), smooth exine and lack of a notch in the amb.

*Melaleuca ericifolia*

Grains have straight to slightly concave sides, the amb is rounded and notched at the base of the vestibule (Fig. 4C). Colpi are curved, enclosing a small apocolpium or rarely a polar island about 1μm diameter. The colpi have rough edges and thickened margins about 1μm wide. The exine is smooth around the colpal region and is scabrate (Fig. 11H) in the equatorial mesocolpal regions. There is some variation in the intensity of the pattern between grains.

Ambs have a distinct vestibule, the inside surfaces are roughened. The floor of the vestibule is straight or slightly concave. The roof of the vestibule is the same thickness as the ektexine elsewhere on the grain. This feature is quite variable with the orientation of the grain, and may not be seen in oblique views. Dimensions are in Table 5.

This species is most like *Melaleuca armillaris* but is distinguished by the scabrate exine pattern and the notches at the base of the vestibule (Table 5). This species is also like *M. thymifolia* but has thickened colpi margins.

*Melaleuca nodosa*

Grains have straight or slightly concave sides. The amb is rounded. Colpi are straight or slightly curved, and the edges are distinctly roughened. The bifurcations of the colpi enclose a large polar island 7-8μm diameter. Exine has a very fine, distinct, granular/scabrate pattern (Fig. 11F).

Ambs have a distinct vestibule. The separation of the two layers of the exine is relatively narrower than that seen on other species. The inside surfaces of the vestibule are roughened. The floor is straight or slightly concave; this variation is partly due to the aspect of viewing. The roof has a tendency to curve inwards at the edges of the exopore. The ektexine over the vestibule is unthickened and is finely scabrate, like the rest of the exine (Fig. 12Q).

The colpi are unusually distinct in this species. This species is most like *Melaleuca quinquenervia* but is distinguished by its larger polar island (Table 5).

*Melaleuca quinquenervia*

Grains have straight to slightly concave sides and rounded ambs. Colpi are angular and enclose a distinct polar island 3-5μm diameter (Fig. 12R). The polar island has the same ektexine as the rest of the grain and fits the apocolpium closely (Fig. 5A). The colpi have smooth edges and have thickened margins up to 1μm wide. The exine is smooth.

Ambs have a distinct vestibule with roughened inner surfaces. The floor of the vestibule is straight to convex. The roof of the vestibule is the same thickness as the ektexine elsewhere on the grain and has a smooth outer surface. Dimensions are in Table 5.

This species is most like *Melaleuca nodosa* but is distinguished by its smaller polar island (Table 5).

*Melaleuca thymifolia*

Grains have concave sides, the amb is rounded and may have notches at the base of the vestibule. Colpi are straight and are either syncolpate or enclose an apocolpium, with a maximum diameter of 1μm. There is no visible thickening to the edges of the colpi which are irregular. The exine has a faint scabrate pattern all over the grain.

The ambs have a distinct vestibule with the inner surfaces roughened. The floor of the vestibule is flat or slightly concave. The roof thins towards the exopore and is never thicker then the ektexine elsewhere on the grain. The outer surface of the pore has a faint scabrate pattern. Dimensions are in Table 5.

This species is most similar to *Melaleuca ericifolia* but the sides of the amb are markedly concave and there are thickened margins to the colpi (Table 5). This species is also similar to *Melaleuca armillaris* but the colpi are straight and the visible polar membrane is <1μm wide (Table 5).

## Intraspecific Variation

As noted in the descriptions, there is considerable variation in the colpi and apocolpia of the *Angophora*/bloodwood group. In this group, breaks in the colpi are a striking characteristic. A detailed analysis of this variation is presented here.

Five specimens of *Eucalyptus gummifera*, one other bloodwood, *E. eximia*, and two species of *Angophora* have been analysed in detail. Twenty grains of each specimen have been examined and as the two sides of the grain may be quite different, both sides have been recorded so that there are 40 observations for each specimen. Figures 5B, 6, 8 and 9 show the range of variation and Table 7 summarises the observations.

From Table 7 it can be seen that only one specimen of *E. gummifera*, 2061, has predominantly complete colpi. Three of the specimens have broken colpi as the major form of variation. Colpal irregularities about the polar membrane is the main form of variation in the remaining specimen, 2029.

The other three specimens of the *Angophora*/bloodwood group (Table 7) show similar variability. All of the specimens have more than one form of variation. Additional species of this group have been examined and they exhibit similar variation.

This variation, and in particular the breaks in the colpi, has not been observed in any *Eucalyptus* species nor in the *Angophora*/bloodwood group. However, one species of the *Leptospermum* group, *L. juniperinum*, has very rare colpi gaps which are small and only one gap per grain has been observed.

## The Identification of Species and Genera

Species are only regarded as successfully separated if two or more easily observed character states are different in each species. All of the species have been separated successfully with the exception of *Eucalyptus gummifera* and *Angophora hispida*. In this case, the only useful characters are the apex/base measurement, where the ranges overlap, and the wall thickness measurements which are regarded as not sufficiently different to be reliable. For these reasons these two species have not been separated. It may be possible, however, to ascribe a probability to a certain grain belonging to one of the species.

Tables 3 to 6 summarise the character states used to distinguish the species. There are sufficient of the more conspicuous characters to effect these distinctions although there may be additional useful characters (see descriptions).

The species observed have been divided into groups, some of which coincide with the genera. Table 2 shows the character states used to define these groups. The smaller and less conspicuous characters are most useful for this purpose. The larger and more conspicuous characters usually show considerable variation so that the range of one group overlaps that of another.

These groups are distinguished by two or more character states with the exception of *Melaleuca* and Other *Eucalyptus* species. With these two groups only one character, viz. the thickened roof over the vestibule, exhibits no overlap. The separation of the Other *Eucalyptus* species and *Melaleuca* groups has not been very successful on the basis of characters shown in Table 2.

An alternative method useful for identification of the groups involves the construction of keys. A fairly small number of characters are required for this purpose. With this method a better separation of *Melaleuca* from *Eucalyptus* is achieved when compared with that in Table 2. However these keys should not be used alone and an identification should be checked out with the full species description. It should be pointed out that these keys apply to this specific reference set of species. With this particular set, a good separation of species has been achieved. However, there may be other species not in this reference set which may be confused with those described here.

## Discussion

The methods adopted in this study have been successful in separating all of the pollen of the myrtaceous species except for two, where the character states overlap. The use of a number of fine-detail characters as well as those of gross morphology has been the key to this success. The reference set is limited to 20 species found within a given area. If other species are included, then the separation may not be as good as that achieved here.

The pollen of the *Angophora*/bloodwood group shows breaks and other irregularities of the colpi. The type of irregularity and its frequency vary with the specimen. This character has not been used for the purpose of separating the species. Obviously, intraspecific variation must be assessed and those characters which exhibit it excluded for this purpose.

The species may be divided into groups, some of which coincide with genera. However, as only a few species from each genus is included in this study, the character states used to define the genus here are not a reliable guide to the genus as a whole.

This study uses tables and keys as aids to identification. Other methods, e.g. punch cards or a computer program could be equally useful. With a larger reference set, the use of a computer program would be a definite advantage.

The methods described here are relatively time consuming, especially in the documentation of character states. A palynologist whose chief interest is the history of past vegetation may begrudge the time required for this documentation. However, the subjective 'picture matching' method of identification is unsuitable for pollen which is superficially very similar.

Myrtaceous pollen is found throughout the Tertiary and a total of nine form genera have been described. *Myrtaceidites eucalyptoides* forma convexus Cookson and Pike 1954, lacking polar islands, is most like the *Angophora*/bloodwood type described here. *M. eucalyptoides* forma orthus Cookson and Pike 1954 is very similar but has polar islands of variable size. It is probably also a *Eucalyptus* species (Martin, unpubl.). Some of the other form-species may also contain *Eucalyptus* species. The approach adopted here could be, and should be applied to Tertiary pollen, but the reference set would have to include a good representation of most genera in the family.

These methods adopted for myrtaceous pollen could be applied to other groups of similar pollen, e.g. tricolpate and tricolporate grains.

## Key to the Subdivision of the Pollen of the Myrtaceae Studied in the Jibbon Area

| | | |
|---|---|---|
| A | Apex/base > 30µm | *Angophora*/bloodwoods |
| A* | Apex/base > 30µm | |
| B | Colpi edges broken | *Angophora*/bloodwoods |
| B* | Colpi edges rough | |
| C | Roof of vestibule thickened | *Eucalyptus* |
| C* | Roof of vestibule not thickened | |
| D | Colpi edges thickened | *Melaleuca* |
| D* | Colpi edges not thickened | |
| E | Colpi edges smooth | |
| F | Colpi arcuate | *Eucalyptus sieberi* |
| F* | Colpi angular | *Leptospermum* |
| E* | Colpi edges rough or irregular | |
| G | Large polar island 6-8µm | *Melaleuca nodosa* |
| G* | No polar island | |
| H | Vestibulum roof thins gradually towards pore opening | *Melaleuca thymifolia* |
| H* | Vestibulum roof is truncate at pore opening | *Leptospermum* |

## Key to the Subdivision of the *Angophora*/Bloodwood Group

| | | |
|---|---|---|
| A | Exine pattern of vermiculate grooves | *Angophora costata* |
| A* | Exine pattern smooth or slight undulations | |
| B | Edges of colpi irregular, vestibule large and clear | *Eucalyptus eximia* |
| B | Edges of colpi rough, vestibule small and indistinct | *Eucalypatus gummifera* *Angophora hispida* |

### KEY TO THE SUBDIVISION OF THE *EUCALYPTUS* GROUP

| | |
|---|---|
| A Roof of the vestibule not thickened | *Eucalyptus sieberi* |
| A* Roof of vestibule thickened | |
| B Exine pattern vermiculate | *Eucalyptus obstans* |
| B* Exine pattern scabrate or smooth | |
| C Angle of amb rounded | |
| D Colpi angular | *Eucalyptus camfieldii* |
| D* Colpi arcuate | *Eucalyptus leuhmanniana* |
| C* Notch at base of vestibule | |
| E Polar island 4-9µm, with the same ektexine as the rest of the grain | *Eucalyptus botryoides* |
| E* Polar island with rugulate/granulate ektexine or polar membrane with granules | *Eucalyptus haemastoma* |

### KEY TO THE SUBDIVISION OF THE *MELALEUCA* GROUP

| | |
|---|---|
| A Colpi straight/angular | |
| B Polar island 3-5µm, colpi edges thickened | *Melaleuca quinquenervia* |
| B* No polar island, colpi edges not thickened | *Melaleuca thymifolia* |
| A* Colpi arcuate | |
| C Polar island 7-8µm, colpi edges not thickened | *Melaleuca nodosa* |
| C* No polar island or rare polar island <2µm, diameter, colpi edges thickened | |
| D Exine pattern scabrate in mesocolpal areas, smooth around colpi, colpi edges rough | *Melaleuca ericifolia* |
| D* Exine smooth, colpi edges smooth | *Melaleuca armillaris* |

### KEY TO THE SUBDIVISION OF THE *LEPTOSPERMUM* GROUP

| | |
|---|---|
| A Exine patterning verrucate | *Leptospermum arachnoides* |
| A* Exine patterning smooth or scabrate | |
| B Colpi do not meet at the pole | |
| C Exine smooth | *Leptospermum juniperinum* |
| C* Exine scabrate or verrucate | *Leptospermum arachnoides* |
| B* Colpi meet at pole | |
| D Edges of colpi smooth | |
| E Inside surfaces of vestibule rough, exine scabrate | *Leptospermum polygalifolium* |
| E* Inside surfaces of vestibule smooth, exine smooth | *Leptospermum juniperinum* |
| D* Edges of colpi rough | |
| F Inside surfaces of vestibule rough, apex/base measurement 17.6 to 20.6µm | *Leptospermum laevigatum* |
| F* Inside surfaces of vestibule smooth, apex/base measurement 13.7 to 15.7µm | *Leptospermum trinervium* |

## ACKNOWLEDGMENTS

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TABLE 1
*Specimens selected for study.*
Pollen slide number in the Modern Pollen Collection. School of Biological Sciences, University of New South Wales. All locations are in New South Wales. All authorities after Harden, 1991.

| Group | Species | Slide No. | Pollen Locality | Collection |
|---|---|---|---|---|
| *Angophora*/bloodwood | *Angophora hispida* (Smith) Blaxell | 2058 | Marley track, Bundeena Rd., Royal Nat. Pk. | C. Bartlett, 13. ix. 1997, UNSW7074, (UNSW) |
| | *Angophora costata* (Gaertner) Britten | 2011 | Big Gibber. | B. Fox, 1979, UNSW9311, (UNSW) |
| | *Eucalyptus eximia* Schauer | 2066 | Between Maryala and Glenorie. | J.T. Waterhouse, 29.x.1967, (UNSW) |
| | *Eucalyptus gummifera* (Sol. ex Gaertner) Hochr. | 2060 | Ouringham, Pacific Hwy. | K.R. Brown, 22.ii. 1969, (UNSW) |
| | | 2062 | Jibbon Swamp, Royal Nat. Pk. | J.M. Chalson, April 83, UNSW14535, (UNSW) |
| | | 1721 | Bungwahl, Tea Gardens | J.T. Waterhouse, 28.ii.1983, UNSW5474, (UNSW) |
| | | 2061 | French's Forest | D. Blaxell, 31.i.1938, (UNSW) |
| | | 2029 | Heathcote | J.T. Waterhouse, 2.iii.1969, UNSW121, (UNSW) |
| *Eucalyptus* | *Eucalyptus botryoides* Smith | 2010 | Kangaroo Creek Nat. Pk. | J. Camfield, (NSW) |
| | *Eucalyptus camfieldii* Maiden | 2008 | Warumbul Turnoff, Royal Nat. Pk. | J.T. Waterhouse, 1969, UNSW829, (UNSW) |
| | *Eucalyptus haemastoma* Smith | 2063 | Mona Vale | J.T. Waterhouse, 10.v.1967, UNSW380, (UNSW) |
| | *Eucalyptus luehmanniana* F. Meull. | 2059 | Kuring-gai Chase | D. Blaxell, 19.v.1964, (UNSW) |
| | *Eucalyptus obstans* L. Johnson & K. Hill | 2064 | Sir Betram Stevens Dr. turnoff to Wattamolla, Royal Nat. Pk. | D. Blaxell, 11.viii.1964, (UNSW) |
| | *Eucalyptus sieberi* L. Johnson | 2031 | Fire trail en route to Faulconbridge Point, Blue Mts. Nat. Pk. | B. Wiecek and B.S. Wannen, 10.x.1982, UNSW14135, (UNSW) |
| *Melaleuca* | *Melaleuca armillaris* (Sol. ex Gaertner) Smith | 2012 | Royal Nat. Pk. | K.M. Winterhalder, 1972, (UNSW) |
| | *Melaleuca ericifolia* Smith | 2026 | Dee Why Lagoon | K.M. Winterhalder, 15.ix.1982, UNSW13978, (UNSW) |
| | *Melaleuca nodosa* (Sol. ex. Gaertner) Smith | 2013 | La Perouse | A.S. Murray, 1978, UNSW3780, (UNSW) |
| | *Melaleuca quinquenervia* (Cav.) S.T. Blake | 2027 | North Head Res. Manly | A.D. Chapman, 16.iv.1968, (UNSW) |
| | *Melaleuca thymifolia* Smith | 2028 | Track to Meelong Swamps — Tari Creek, (nr. Colo River) | S. Francis, 15.vi.1981, UNSW12024, (UNSW) |
| *Leptospermum* | *Leptospermum arachnoides* Gaertner | 2022 | North Head | D. Blaxell, 29.xi.1957, (UNSW) |
| | *Leptospermum trinervium* (Smith) J. Thompson | 2021 | Bowan's Creek Rd., 0.8km from Bell's Line of Road | C. J. Quinn and J.T. Waterhouse, 14.xi.1975, UNSW5360, (UNSW) |
| | *Leptospermum polygalifolium* Salisb. | 2023 | North Marley Track, Royal Nat. Pk. | K.M. Winterhalder, 2.xi.1972, UNSW3017a, (UNSW) |
| | *Leptospermum juniperinum* Smith | 2065 | Smith's Lake | General Ecology Excursion, 17.v.1979, UNSW6815, (UNSW) |
| | *Leptospermum laevigatum* (Gaertner) F. Muell | 2024 | Site 132 TMH, Worrain Beach | T.M. Howard, 29.ix.1979, (UNSW) |

TABLE 2

*Comparison of the Pollen of the* Myrtaceae *groups studied*

* (single exception to the group)

| Group name | No. of species | Notch at Base of vestibule | Colpi | Type of colpal edge | Roof of vestibule | Apocolpium size (μm) | Polar island | Exine patterning | Apex/base (range μm) | Inside surface of vestibulum | vestibulum |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 *Leptospermum* | 5 | no | angular | smooth or rough | thin | <1 | no | granulate/scabrate (verrucate, smooth, granular)* | 12.7-22.5 | rough or smooth | indistinct |
| 2 *Melaleuca* | 5 | yes or no | arcuate or angular | rough or irregu-lar maybe thickened | thin | 0-8 | yes or no | smooth or faint scabrate | 16.7-22.5 | rough | clear |
| 4 *E. sieberi* | 1 | yes | arcuate | smooth | thin | 4 | no | scabrate | 18.0-23.0 | smooth | clear |
| 3 *Angophora*/bloodwood | 4 | yes or no | arcuate and variable | irregular or broken or rough | thickened | 0-10 | yes | undulate or vermiculate | 23.5-46.1 | rough | clear or indistinct |
| 5 Other *Eucalyptus* species | 5 | yes or no | angular (arcuate) | rough | thickened | 4-9 | yes or no | scabrate (vermiculate) | 19.6-28.0 | rough | indistinct (clear) |

TABLE 3

*Comparison of the Pollen of the* Angophora/ *bloodwood Species studied*

| Species | Edges of colpi | Mesocolpal exine pattern | Pore vestibuilum | Apex/base range μm (mean) | Pore width range μm (mean) | Pore height range μm (mean) | Wall width range μm (mean) |
|---|---|---|---|---|---|---|---|
| *A. costata* | irregular | vermiculate grooves | small, clear | 32.0-38.0 (35.0) | 4.9-6.9 (6.2) | 3.9-4.9 (4.2) | 2.0-2.9 (2.2) |
| *A. hispida* | broken | undulate | small, indistinct | 26.5-35.3 (31.3) | 3.9-8.8 (5.4) | 4.9-6.9 (5.5) | 2.9-4.4 (2.2) |
| *E. gummifera* | broken | undulate | small, indistinct | 33.0-40.0 (36.0) | 5.9-9.8 (8.1) | 3.4-5.9 (4.1) | 1.5-2.9 (2.4) |
| *E. eximia* | irregular, rough | vermiculate grooves | medium, indistinct | 23.5-27.0 (25.2) | 5.4-7.4 (6.3) | 2.9-4.4 (3.4) | 2.0-2.9 (2.2) |

TABLE 4

*Comparison of the Pollen of the* Eucalyptus *Species studied.*
* not over pore area

| Species | Notch in amb | Colpi | Variation in exine pattern* | Exine pattern Thickness (mean µm) | Apocolpium | Roof of vestibule | Inner surface of vestibule Pore width (mean µm) | Pore height (mean µm) | Apex/base (mean µm) |
|---|---|---|---|---|---|---|---|---|---|
| *E. sieberi* | yes | arcuate | smooth at colpal edges | scabrate 1.0-1.5 (1.3) | smooth polar membrane | thin | smooth 3.9-7.8 (5.4) | 1.0-2.0 (1.2) | 18.0-23.0 (20.0) |
| *E. botryoides* | yes | angular | even over grain | scabrate 1.5-2.0 (1.8) | polar island 4-9 | thickened | rough 2.9-5.9 (4.6) | 1.0-2.9 (2.0) | 24.0-27.0 (25.6) |
| *E. camfieldii* | no | angular | smooth at colpal edges | scabrate 1.5-2.9 (1.7) | smooth polar membrane | thickened | rough 2.9-5.9 (4.8) | 1.0-2.0 (1.5) | 23.5-27.4 (26.0) |
| *E. luehmanniana* | no | arcuate | more pronounced at colpal edges | smooth to faint scabrate 1.0-2.0 (1.5) | polar island 3-6 or brevicolpate with rugulate/granulate area | thickened | rough 3.9-5.9 (4.8) | 2.9-3.9 (3.4) | 19.6-24.5 (22.4) |
| *E. haemastoma* | yes | angular | even over grain | smooth to faint scabrate 1.0-2.5 (1.8) | polar island 3-6 or brevicolpate with rugulate/granulate area or membrane with granules | thickened | rough 5.9-7.8 (6.9) | 3.3-4.9 (4.0) | 21.1-24.5 (22.3) |
| *E. obstans* | yes | angular | more pronounced at colpal edges | vermiculate 1.5-2.5 (1.9) | polar island 7-9 thin granulate ektexine on island | thickened | rough 5.9-7.8 (6.8) | 3.9-5.4 (4.7) | 23.5-27.4 (25.3) |

TABLE 5

*Comparison of the Pollen of the* Melaleuca *Species studied.*

| Species | Sides of amb | Colpi shape edges | Thickened margin of colpi | Polar island diam. | Exine pattern (mean µm) | Notch in amb. | Pore height (mean) Width (mean µm) | Apex/base (mean µm) |
|---|---|---|---|---|---|---|---|---|
| *M. armillaris* | concave | arcuate smooth | yes | no | smooth 1.0-1.5 (1.3) | no | 2.0-3.9 (3.5) 3.9-7.8 (6.0) | 16.7-22.5 (18.9) |
| *M. ericifolia* | straight to slightly concave | arcuate rough | yes | rare <2 | scabrate 1.0-2.1 (1.1) | yes | 1.5-2.9 (2.0) 2.9-4.9 (4.3) | 17.6-20.6 (18.8) |
| *M. nodosa* | straight to slightly concave | arcuate rough | no | yes 7-8 | granular/ scabrate 1.0-1.5 (1.1) | no | 2.0-3.4 (2.7) 2.9-5.9 (4.2) | 16.7-20.6 (18.5) |
| *M. quinquenervia* | straight to slightly concave | angular smooth | yes | yes 3-5 | smooth 1.0-1.5 (1.0) | no | 2.0-2.9 (2.6) 4.9-6.9 (5.5) | 16.7-20.6 (18.8) |
| *M. thymifolia* | concave | straight irregular | no | no | scabrate 1.0-1.5 (1.1) | yes | 2.0-3.4 (2.7) 3.9-5.9 (4.8) | 17.6-20.6 (18.9) |

TABLE 6
*Comparison of the Pollen of the* Leptospermum *Species studied.*

| Species | Exine patterning Thickness (mean µm) | Sides of amb | Apocolpium | Edges of colpi | Vestibule inner surfaces Width (mean µm) | Vestibule floor Height (mean µm) | Exopore edge | Apex/base (mean µm) |
|---|---|---|---|---|---|---|---|---|
| *L. arachnoides* | verrucate to granular/scabrate 1.5-2.0 (1.9) | concave | brevicolpate | smooth | rough 2.5-4.9 (3.8) | flat 2.0-2.9 (2.5) | abruptly rounded | 17.6-22.5 (20.0) |
| *L. polygalifolium* | scabrate over all of grain 1.0-2.0 (1.3) | concave | syncolpate | smooth | rough 2.5-4.9 (3.8) | slightly convex 2.0-2.9 (2.2) | abruptly rounded | 13.7-17.6 (15.2) |
| *L. juniperinum* | smooth 1.0-1.5 (1.0) | concave | syncolpate rare gaps and brevicolpate | smooth | smooth 1.5-2.9 (2.2) | convex 1.5-2.0 (1.7) | gradually tapering | 12.7-14.7 (14.3) |
| *L. laevigatum* | granular/scabrate to smooth at pores 1.0-2.0 (1.5) | straight to slightly concave | syncolpate | rough | rough 2.9-4.9 (4.2) | concave 2.0-2.9 (2.5) | truncate | 17.6-20.6 (19.3) |
| *L. trinervium* | granular/scabrate over all of grain 1.0-1.0 (1.0) | straight to slightly concave | syncolpate | rough | smooth 1.5-2.9 (2.2) | flat 1.5-2.0 (1.7) | abruptly rounded | 13.7-15.7 (14.3) |

TABLE 7
*Intraspecific Variation in the* Angophora/*bloodwood Group.*
* Occurring together in one grain

| Species | Colpi complete Fig. 6B % | Incomplete Colpal gaps Fig. 8A, B, C % | Poor definition polar membrane Fig. 9A, B, C, D % | Poor definition of colpi Fig. 9E, F, G % | Small polar island Fig. 5B and 8A* % | Brevicolpate Fig. 6D % |
|---|---|---|---|---|---|---|
| *E. gummifera*, 2062 | 7.5 | 87.5 | 5 | | | |
| 2029 | 17.5 | | 22.5 | 42.5 | 15.0 | 2.5 |
| 2061 | 45.0 | 37.5 | 15.0 | 2.5 | | |
| 1721 | 7.5 | 92.5 | | | | |
| 2060 | 12.5 | 85.5 | 2.5 | | | |
| Average, *E. gummifera* | 18.0 | 60.5 | 9.0 | 9.0 | 3.0 | 0.5 |
| *E. eximia* | 92.5 | 7.5 | | | | |
| *A. hispida* | 10.0 | 82.5 | 2.5 | | 2.5 | 2.5 |
| *A. costata* | 52.5 | 22.5 | 2.5 | | 22.5 | |

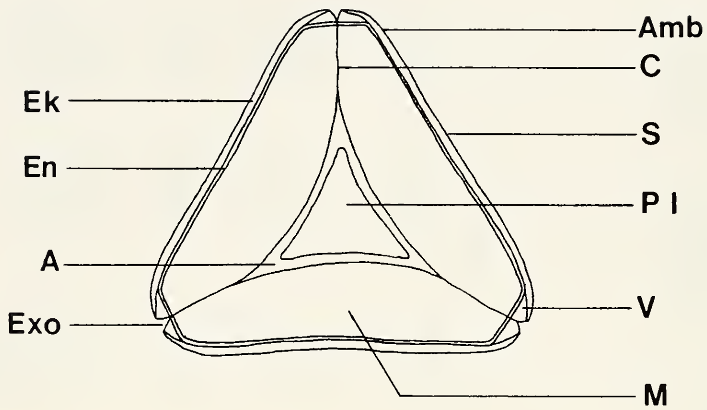


*Fig. 1.* Generalised Myrtaceae pollen grain, polar view. Ek. Ektexine; En, Endexine; A, Apocolpium; Exo, Exopore; Amb, The amb; C, Colpus; S, Sides of amb; P I, Polar island; V, Vestibule; M, Mesocolpal region.

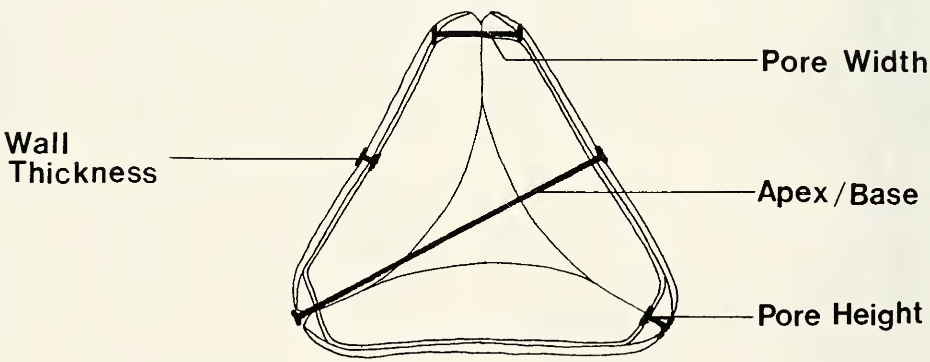


*Fig. 2.* Measurements made on pollen grains.

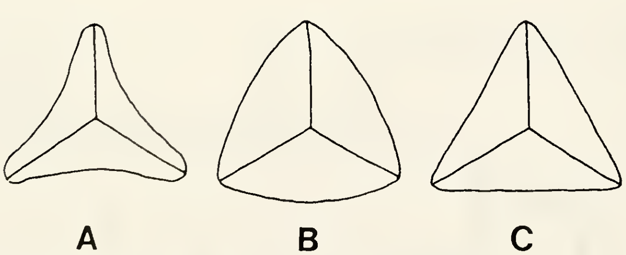


*Fig. 3.* Sides of pollen grains: A, concave; B, convex; C, straight.

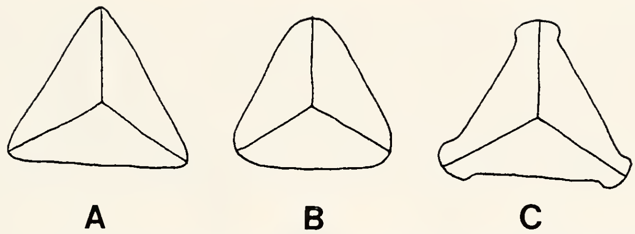


*Fig. 4.* Angle of the amb and notch at the base of the vestibule: A, sharply rounded angle; B, rounded angle; C, rounded angle with a notch at the base of the vestibule.

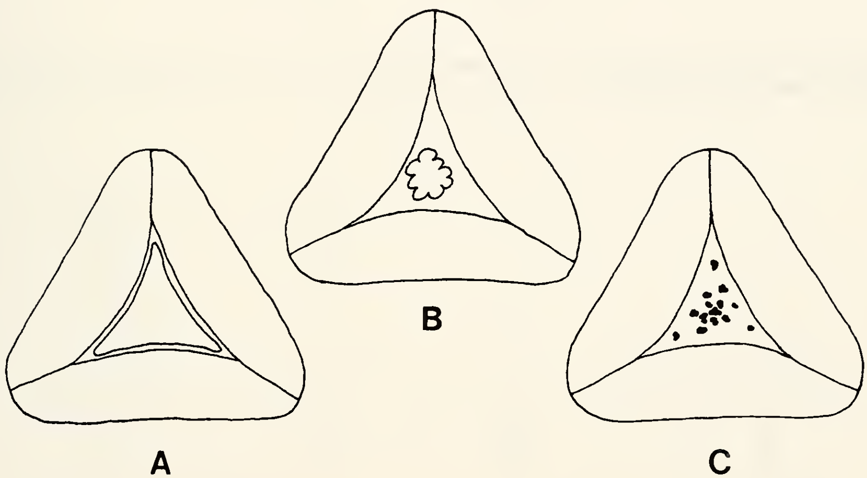


*Fig. 5.* Types of apocolpia: A, apocolpium with closely fiiting polar island; B, apocolpium with small irregular polar island; C, apocolpium with granules on the polar membrane.

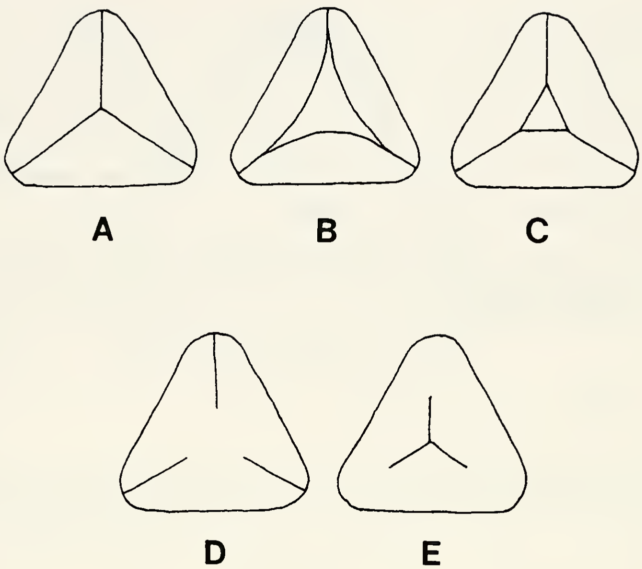


*Fig. 6.* Types of colpi: A, syncolpate; B, parasyncolpate with arcuate colpi; C, parasyncolpate with angular colpi; D, brevicolpate; E, syndemicolpate.

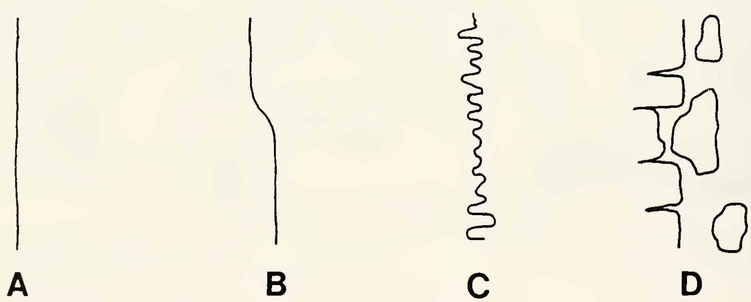


*Fig. 7.* Types of colpal edges; A, smooth; B, irregular; C, rough; D, broken.

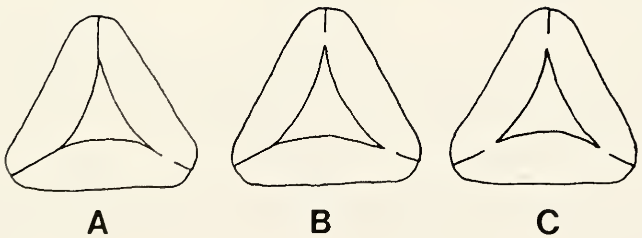


*Fig. 8.* Colpal gaps; A, 1 gap; B, 2 gaps; C. 3 gaps.

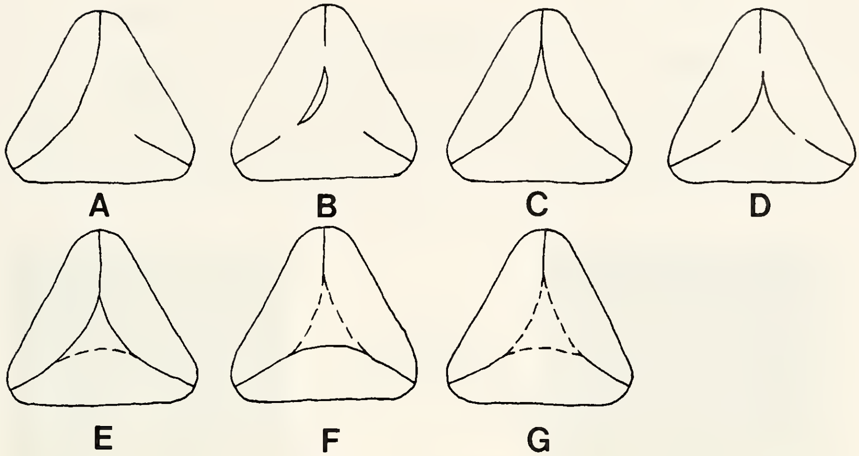


*Fig. 9.* Other colpal irregularities associated with the *Angophora*/bloodwood group: A-D, incomplete definition of apocolpium, with or without colpal gaps; E-G, poor definition of colpi around apocolpium.

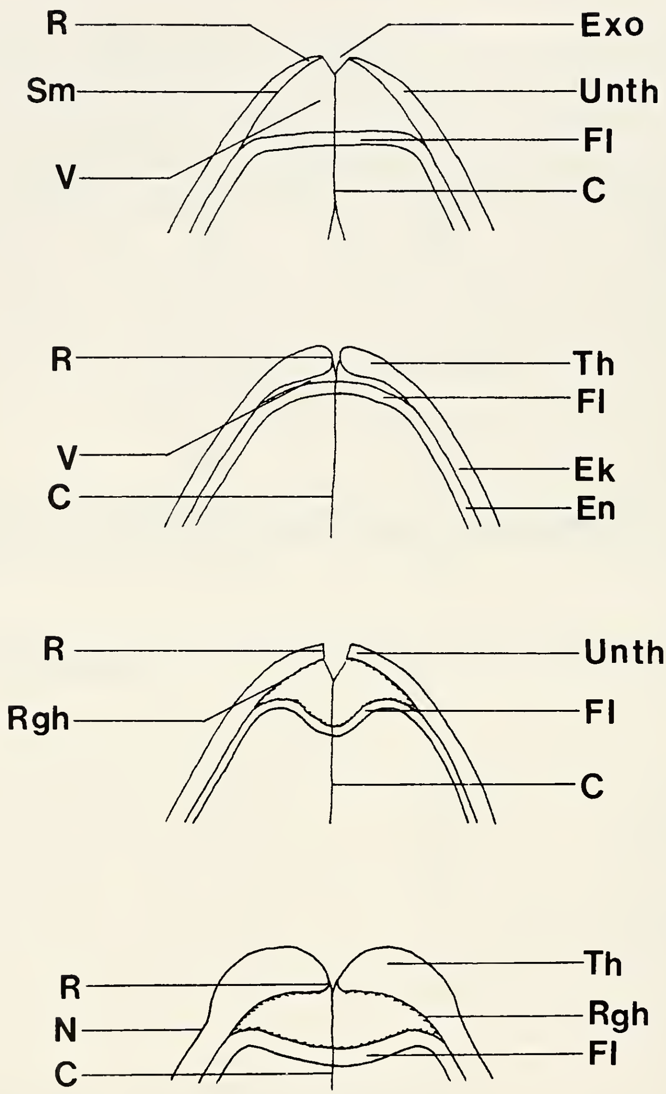


*Fig. 10.* The pore area: A, *Eucalyptus sieberi*; Roof tapers gently to the exopore edge and is unthickened. Vestibule large and inner surface smooth. Floor of vestibule flat. B, *Eucalyptus botryoides*; Thickened roof over small vestibule rounds off abruptly at exopore edge. Floor of vestibule convex, C, *Leptospermum laevigatum*; Roof over small vestibule is unthickened and is truncate at exopore edge. Floor of vestibule concave. D. *Angophora costata*; Roof rounds off abruptly at exopore edge. The amb is notched at the base of the vestibule. Vestibule roof is thickened and has rough inner surfaces. The vestibule floor is concave. C, Colpus; Ek, Ektexine; En, Endexine; Exo, Exopore; Fl, Floor of vestibule; N, Notch at the base of the vestibule; R, Roof of vestibule; Rgh, Rough inner surfaces of vestibule; Sm, Smooth inner surfaces of vestibule; Th, Thickened roof of vestibule; Unth, Unthickened roof of vestibule; V, Vestibule.

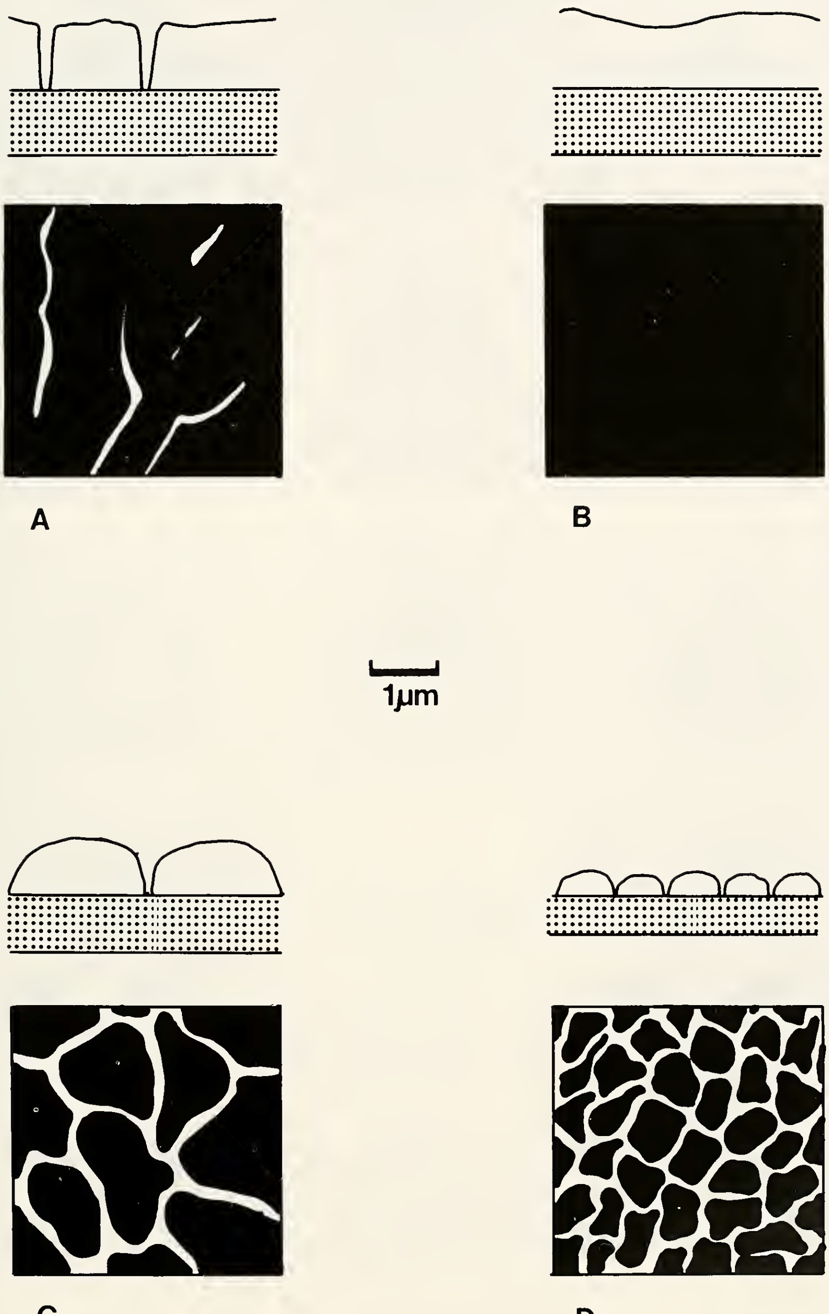


*Fig. 11.* A–D. Types of exine pattern. Optical section with plan view below. Scale bar indicates 1 µm; A, vermiculate patterning of *Angophora costata*; B, undulate patterning of *Eucalyptus gummifera*; C, verrucate patterning of *Leptospermum arachnoides*; D, verrucate/scabrate patterning of *Leptospermum arachnoides*.

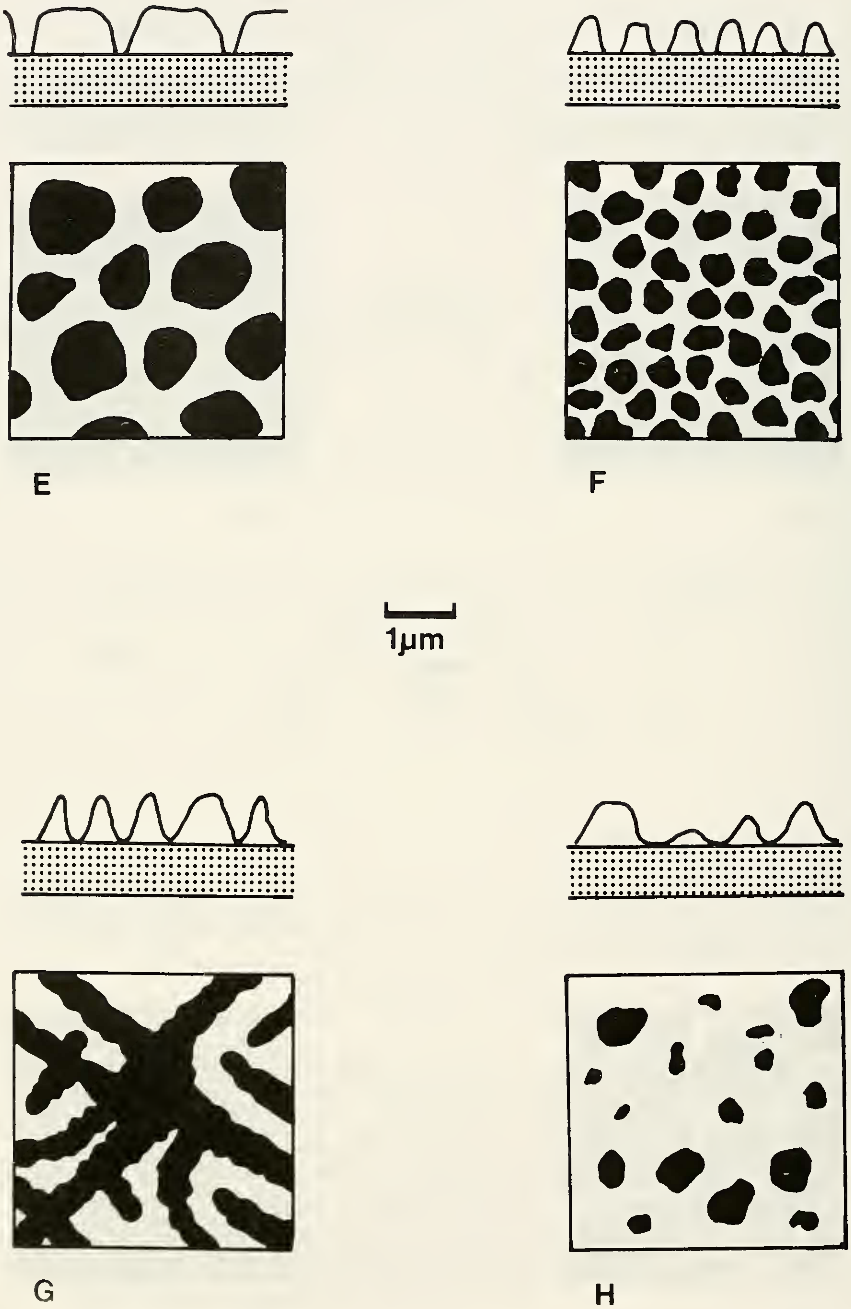


*Fig. 11.* E–H. E, granulate patterning of *Leptospermum trinervium*; F, granulate/scabrate patterning of *Melaleuca nodosa*; G, rugulate patterning of *Eucalyptus luehmanniana*; H, scabrate patterning of *Melaleuca ericifolia*.

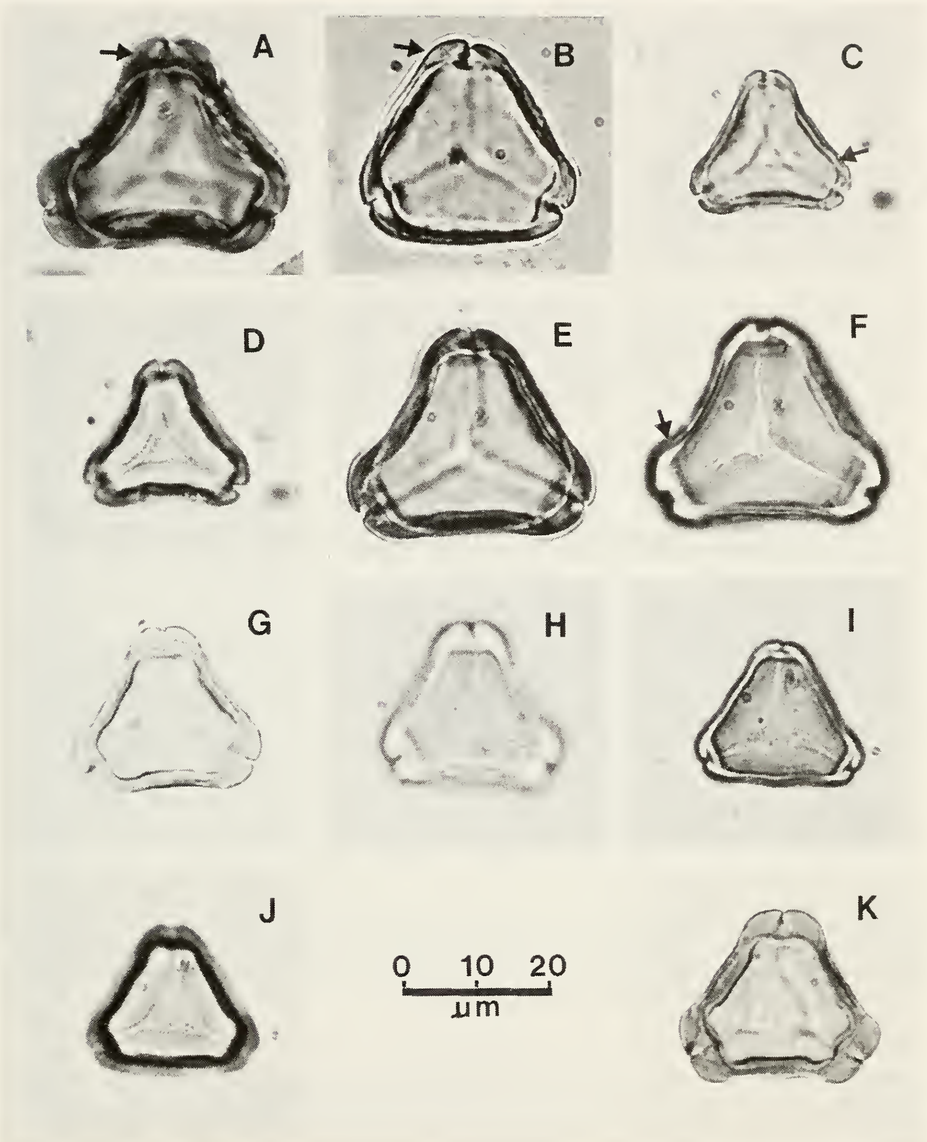


*Fig. 12.* A—K. All photographs are from untouched negatives. A, *Angophora hispida*, showing roughened inner surfaces of vestibule and undulate exine pattern. B, *Angophora costata*, showing thickened pore roof and concave vestibule floor. C, *Eucalyptus eximia*, showing slightly thickened pore roof and small vestibule. D, *Eucalyptus eximia*, showing rough colpal edges. E, *Eucalayptus gummifera*, showing flat vestibule floors. F, *Eucalyptus gummifera*, showing colpal gaps. G, *Eucalyptus haemastoma*, showing thickened pore roof. H, *Eucalyptus haemastoma*, showing rough colpal edges and angular colpi. I, *Eucalyptus luehmanniana*, showing faint scabrate patterning in mesocolpal areas. J. *Eucalyptus luehmanniana*, showing membrane with granules in the apocolpium. K, *Eucalyptus obstans*, showing greatly thickened vestibule roof.

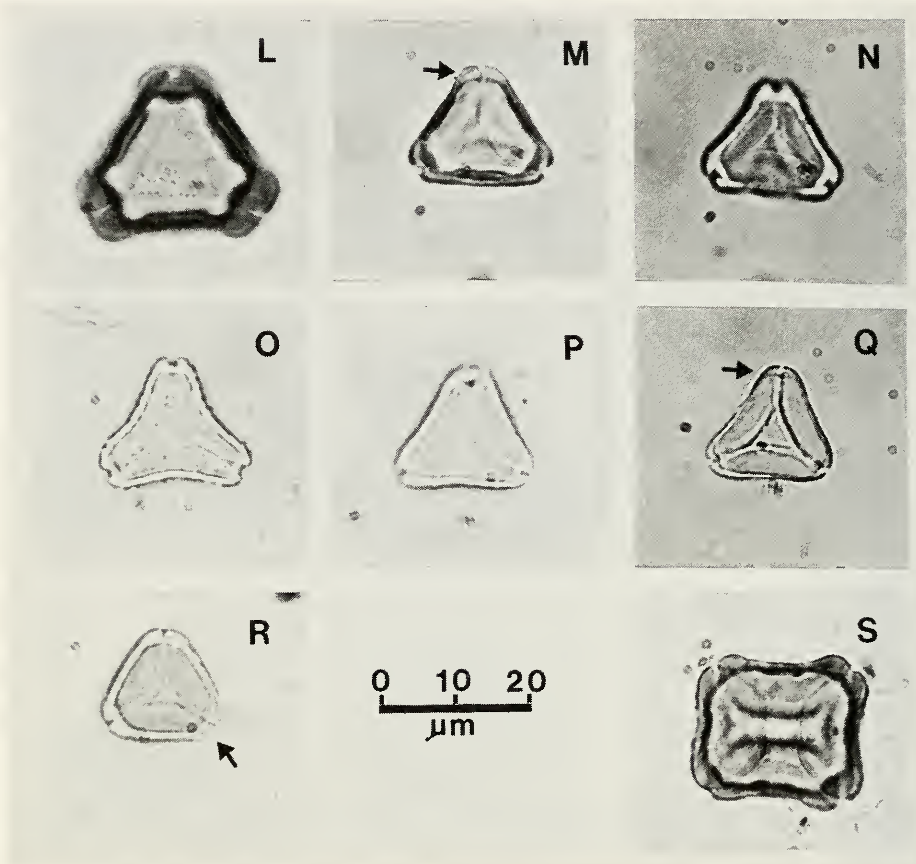


*Fig. 12.* L–S. L, *Eucalyptus obstans,* showing broken edges of colpi and vermiculate grooves in the exine. M, *Eucalyptus sieberi,* showing thin pore roof. N, *Eucalyptus sieberi,* showing scabrate exine pattern. O, *Leptospermum arachnoides,* showing brevicolpate morphology and verrucate exine pattern. P, *Leptospermum laevigatum,* showing syncolpate morphology and granular/scabrate exine pattern. Q, *Melaleuca nodosa,* showing a large polar island and thin-roofed vestibule. R, *Melaleuca quinquenervia,* showing a smaller polar island and thin tapering roof of the vestibule. S, *Eucalyptus haemastoma,* abnormal four-pored grain.

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